

WEB ORIENTATION OF THE BANDED GARDEN SPIDER *ARGIOPE TRIFASCIATA* (ARANEAE, ARANEIDAE) IN A CALIFORNIA COASTAL POPULATION

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ABSTRACT. Magnetic heading (direction the spider's ventrum faced) and web inclination (degree of slant from the vertical) in *Argiope trifasciata* Forskål, a diurnal orb-weaving spider, were studied at a coastal site in southern California for nine weeks in fall 1999. Throughout the study, *A. trifasciata* largely occupied east-west oriented webs with their venters facing south and southwest. Mean magnetic heading was unaffected by ambient temperature extremes. Inclination levels varied from week to week over an approximately 5° range. However, these changes followed no discernible pattern and were independent both of the sun's decrease in maximum altitude during the course of the study and of magnetic heading. Since the ventrum of *A. trifasciata* is dark, the consistent southern orientation exhibited by spiders at our study site suggests that they sought to maximize solar radiation in an attempt to gain heat. In addition, the east-west, facing-the-sun orientation of webs at this site places them parallel to the prevailing western breezes, minimizing their exposure to wind disturbance. As for inclination, it is unclear what factors may be influencing the degree of slant in *A. trifasciata* webs and further study will be needed to ascertain what they might be.

Keywords: Araneidae, *Argiope trifasciata*, web orientation, web inclination, solar radiation

For diurnal web building spiders which may occupy partially to fully exposed positions in their webs for long periods, thermal stress due to excessive heating by the sun or exposure to low temperature conditions could be a significant problem. Spiders from a variety of taxa have demonstrated web orientations which minimize or maximize insolation for the resident spiders. For example, Riechert & Tracy (1975) documented how the funnel webs of the desert agelenid *Agelenopsis aperta* (Gertsch 1934) are oriented to limit exposure to direct sunlight during the day. Biere & Uetz (1981) found that the orb webs of the forest araneid *Micrathena gracilis* (Walckenaer 1805) were oriented in a north-south plane (spiders facing east-west) in warm, well lit microhabitats, while webs in cool, shaded microhabitats had an east-west orientation (spi-

ders facing north-south). Such orientations would minimize the amount of body surface subject to insolation at midday for spiders in the well lit, warm microhabitats and would maximize the amount of body surface exposed to the sun's rays at midday for spiders in the shaded, cool microhabitats (Higgins & Ezcurra 1996). This method of modifying heat load via web directional orientation will be considered a form of thermoregulation in this paper. Spiders from a variety of taxa have also been shown to make deliberate postural adjustments while in their webs which act to reduce or increase their exposure to insolation (Pointing 1965; Krakauer 1972; Robinson & Robinson 1973, 1974, 1978; Tolbert 1979; Biere & Uetz 1981; Suter 1981; Higgins & Ezcurra 1996).

Web orientations interpreted as responses to conditions of high or low ambient temperatures and insolation have been reported for the large araneids *Argiope trifasciata* Forskål 1775 (Tolbert 1979) and *Nephila clavipes* (Linnaeus 1767) (Krakauer 1972; Carrel 1978; Higgins & Ezcurra 1996). However, in the case of *N. clavipes*, other studies have failed to find a relationship between web orientation

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and insolation (Robinson & Robinson 1974; Higgins & McGuinness 1991), suggesting regional variation in the use of web orientation as a thermoregulatory response in the Araneidae.

To explore this possibility further, this study examines whether the orb webs of *A. trifasciata* at a southern California locality might be oriented non-randomly with respect to solar radiation. As prior knowledge of web orientation in *A. trifasciata* is limited to two works conducted exclusively in temperate old field habitats east of the Mississippi (Coventry 1967; Tolbert 1979), we were interested in learning whether spiders at our Pacific coast study site would demonstrate any of the web orientation patterns seen in *A. trifasciata* (and other orb weaving taxa) elsewhere.

METHODS

Study species.—The banded garden spider, *A. trifasciata*, is abundant in the United States and its large orb webs are common in the vegetation of fields, gardens and roadsides (McNett & Rypstra 1997; Ramirez & Haakonsen 1999). *Argiope trifasciata* has an annual life-cycle; spiderlings emerge from overwintering eggsacs in spring and adults may be collected from summer to early fall (McReynolds & Polis 1987). Their web is a standard orb, composed of radii, sticky spirals, supporting frames, and sometimes stabilimenta (see Tso 1999 for a detailed description). The resident spider normally hangs head down from beneath the hub of the web, which is typically inclined slightly from the vertical (Tolbert 1975). In this paper, we will refer to the web face from which the spider hangs as the web underside (following Robinson & Robinson 1978) and the opposite face as the web upperside.

Study site.—The study population inhabited the undeveloped, elongate dune system at the western edge of the Ballona property adjacent to Playa del Rey, California, owned by Playa Capital Company, LLC. Located less than 0.5 km from the Pacific Ocean, the 372 m long dune system is bounded on the west by a linear series of apartment complexes sitting atop an approximately 3.7 m high berm, on the north by the Ballona Creek Channel, on the east by wetlands, and on the south by dirt roads (Schreiber 1981). We found webs primarily in coastal dune vegetation such as

bush lupine (*Lupinus arboreus*, *L. chamissonis*), as well as in wetlands pickleweed (*Salicornia subterminalis*, *S. virginica*) along the eastern dunes/wetlands boundary.

Web measurements.—The web sites of 124 large immature and adult female spiders were marked with numbered stake flags on Saturdays from 2 October—27 November 1999. The number present in any given week varied from 13–37. When initially discovered, resident spiders were removed from their webs and quickly transported to the laboratory. They were marked with dots of scale model paint along the periphery of the abdominal dorsum using a modification of the 1—2—4—7 numbering system of Brussard (1971), with each spider being marked to match its respective web site number. Marked spiders were returned to their webs as soon as possible, usually within 3 hr after capture. However, once the study was underway, we periodically discovered evidence of the partial loss of marker dots from some individuals, casting doubt on the reliability of field identification of individuals. In addition, our study site was vandalized and some marker flags were destroyed or moved. Consequently, this study focuses on changes in web orientations from week to week for the population as a whole, following Carrel (1978).

The web parameters measured were magnetic heading (the compass direction of the ventrum of the spider) and web inclination (degree of slant from the vertical). Magnetic headings were measured using a Suunto compass; the angle of orientation was that of a hypothetical dorsal-ventral line emerging from the spider's ventral side (as in Tolbert 1979), with reference to a north compass orientation of 0°. Inclination was determined using a protractor-plumb bob device; the straight edge of the protractor was placed parallel to and near the underside of the slanted web and the angle of the plumb bob string, reflecting the web's deviation from the vertical plane (angle = 0°), was recorded.

Data analysis.—For each week's magnetic heading values, we calculated the mean angle (α) and Rayleigh's r , a measure of the variance around the mean angle, and tested it for significance to determine if the data varied from a uniform circular distribution (Schmidt-Koenig 1975). Homogeneity among the weekly mean angles was analyzed using a multi-

sample Watson-Williams test (Rao & Sengupta, 2001). To see if the magnetic heading data might cluster around the sun’s azimuth at sunrise, sunset or at noon, we conducted V-tests (Zar 1999) for each week’s heading values using the sun’s azimuth for each case (sunrise, sunset, noon). Azimuth data for the nine data collection dates (2 October–27 November) were obtained from the Astronomical Applications Department, U.S. Naval Observatory (<http://aa.usno.navy.mil/AA/data/>).

To determine if magnetic heading was affected by temperature changes over the nine week study, we generated regression plots of mean angle/week vs. the high and low temperatures for the Friday preceding each data collection. While orb-weavers normally build a new web daily (Carico 1986), *A. trifasciata* is not known to work on its web during daylight hours (Tso 1999), and so the webs we visited during our Saturday morning data collections were presumably mostly constructed overnight, perhaps influenced by the temperature conditions of the prior day. The temperature data used here are for Los Angeles International Airport (LAX) (located less than 3.0 km south of the study site), as listed in the weather section of the Los Angeles Times newspaper (<http://www.weatherpoint.com/latimes/>). Temperatures were unavailable for one Friday (5 November), so the regression analyses were based on data for the remaining eight weeks. While the airport is at a higher elevation (≈ 30 m) than the coastal plain which includes the Ballona study site (\approx sea level), long-term records indicate that October–November temperatures are virtually the same for both areas (Felton 1965).

Inclination data have been summarized via weekly means. To determine if these data exhibited any trend during the course of the study, we performed linear regression of mean inclination/week vs. week. In addition, to ascertain if inclination is influenced by the sun’s changing position over time (as implied by Moore 1977), we regressed mean inclination/week against the sun’s maximum altitude (angle from the horizon). Altitude data for the nine sample days (2 October–27 November) were obtained from the Astronomical Applications Department, U.S. Naval Observatory (<http://aa.usno.navy.mil/AA/data/>). Finally, to determine if inclination is related to magnetic

Table 1.—Magnetic heading and web inclination data for *Argiope trifasciata* at Ballona October–November 1999. Sampling dates are in day/month shorthand format. Magnetic heading is with reference to the ventral surface of spiders sitting on webs. Angle refers to degree of slant of the plane of the web from the vertical plane (angle = 0°). Abbreviations: *n* = sample size; α = mean angle (vector); *r* = a measure of the variance around the mean angle, used in the Rayleigh test for unimodality in a sample, for which the respective *P* values are indicated. ** *P* < 0.01; *** *P* < 0.001.

Date	Magnetic Heading			Inclination	
	<i>n</i>	α	<i>r</i>	<i>n</i>	Angle (°)
2 Oct	11	235.73°	0.792***	13	17.54
9 Oct	24	186.53°	0.499**	26	18.73
16 Oct	32	182.60°	0.666***	32	14.59
23 Oct	37	179.93°	0.635***	37	19.84
30 Oct	36	183.48°	0.733***	34	16.82
6 Nov	36	182.91°	0.572***	37	15.08
13 Nov	30	185.81°	0.703***	33	17.70
20 Nov	33	189.90°	0.709***	34	15.12
27 Nov	18	212.67°	0.698***	19	15.95

heading (e.g. Bishop & Connolly 1992), we generated regression plots of inclination vs. magnetic heading using only spiders for which both inclination and heading data were available. These analyses were performed separately by week, as well as for all data combined.

RESULTS

Magnetic heading.—According to the Rayleigh tests, all the samples are non-randomly distributed and all are significantly (*P*’s < 0.001) concentrated toward the S and SW (Table 1). The mean angle varied from 179.93°–235.73°, though for the middle seven weeks (9 October–20 November), it varied over a much smaller range (179.93°–189.90°). However, differences among these samples were non-significant (Watson-Williams test, *P* > 0.05). Hence, throughout this study, *A. trifasciata* occupied east-west oriented webs with the uppersides of webs and venters facing south and southwest.

Solar azimuths and magnetic heading: With all nine samples, the solar azimuths at noon (due south) and sunset (southwest) were both highly consistent with the observed magnetic headings (*P*’s < 0.001), based on the *V*-test

Table 2.—Results of *V*-tests for significant clustering of magnetic heading with respect to the azimuth of the sun at sunrise, noon and sunset. The date format follows Table 1. *Abbreviations:* *n* = sample size; α = mean angle (vector), reproduced from Table 1 for comparison with azimuth values; *AZ* = azimuth; *u* = *V*-test *u* statistic, for which the respective *P* values are indicated. *** *P* < 0.001.

Date	<i>n</i>	α	Sunrise		Noon		Sunset	
			<i>AZ</i>	<i>u</i>	<i>AZ</i>	<i>u</i>	<i>AZ</i>	<i>u</i>
2 Oct	11	235.73°	93.9°	−16.063	180.0°	11.506***	265.8°	17.682***
9 Oct	24	186.53°	97.3°	0.556	180.0°	41.217***	262.6°	9.989***
16 Oct	32	182.60°	100.4°	11.576***	180.0°	85.162***	259.5°	19.316***
23 Oct	37	179.93°	103.5°	23.719***	180.0°	101.054***	256.3°	23.805***
30 Oct	36	183.48°	106.4°	25.033***	180.0°	111.746***	253.5°	38.251***
6 Nov	36	182.91°	109.0°	24.218***	180.0°	87.255***	250.9°	32.738***
13 Nov	30	185.81°	111.5°	22.093***	180.0°	81.261***	248.3°	37.724***
20 Nov	33	189.90°	113.7°	22.668***	180.0°	93.621***	246.2°	57.732***
27 Nov	18	212.67°	115.4°	−4.771	180.0°	31.729***	244.5°	32.026***

results (Table 2). In addition, while the data failed to show significant orientation toward the sunrise azimuth (southeast) on three dates (2 October, 9 October, 27 November), significant orientations were detected on the other six dates (16 October—20 November) (*P*'s < 0.001).

Multiple *V*-tests using a single circular data set and several predicted directions will sometimes indicate consistency with more than one direction, though in such cases, inspection of the magnitude of the *V*-test *u* statistics will indicate which direction is most compatible with the particular data set (examples in Gould & Gould 2002). With *A. trifasciata*, such an approach clearly indicates greatest compatibility with the noon azimuth (due south) for the middle seven weeks (9 October—20 November), as the values of *u* for this azimuth are typically two to four times greater than those for the sunrise and sunset azimuths during this period (Table 2). With the two remaining dates (2 October, 27 November), the *u* values for the sunset azimuth (southwest) are numerically larger than those for the noon azimuth (though only slightly for 27 November), indicating greater compatibility with the heading data. As the mean angles (α 's) for these dates (235.73°, 212.67°, respectively) are more southwesterly than values for any other date (all < 190°), the *V*-test results for these dates are not unexpected. Overall, the *V*-test analyses underscore *A. trifasciata*'s preference for web placement at Ballona with the upper-sides facing south and southwest.

Temperature and magnetic heading: While

Friday temperatures varied widely during the nine weeks of this study (highs: 19.4–31.3 °C; lows: 10–16.1 °C), no significant relationship exists between magnetic heading and either highs (r^2 < 0.0005, *P* = 0.958) or lows (r^2 = 0.003, *P* = 0.895). Magnetic heading at our study site was therefore unaffected by the temperature extremes of the prior day.

Inclination.—Mean inclination values varied randomly from week to week during this study and did not display any trend with time (Table 1; r^2 = 0.161, *P* = 0.284).

Solar altitude and inclination: Analysis of mean inclination values plotted against the sun's maximum altitude for each sample date yields a positive slope (0.116), but this relationship is non-significant (*P* = 0.292), indicating that web placement in the vertical plane was independent of the sun's change in altitude during the course of this study.

Magnetic heading and inclination: No relationship was found between inclination and magnetic heading. This was true for both the nine weekly samples considered individually (r^2 's = 0.0004–0.124, *P*'s = 0.151–0.910), as well as for all data combined (r^2 = 0.002, *P* = 0.471). Hence, the inclination of a web was not influenced by its directional orientation.

DISCUSSION

Magnetic heading.—Our magnetic heading findings for *A. trifasciata* differ somewhat from those of prior investigations. Based on a June–October study of a population in an old field habitat in Tennessee, Tolbert (1979) found that magnetic heading was random for

2/3 of all observations, with significant directionality being seen on selected dates only during the hottest (August) and coldest (October) months. Random magnetic headings during summer (July) have also been described for *A. argentata* (Fabricius) in open grassy areas in Panama (Robinson & Robinson 1978). During Tolbert's (1979) August observations, spiders largely occupied east-west oriented webs with their silver/white dorsums facing south and their dark ventrums facing north, while during October, the situation was reversed, with the dorsums facing north and the ventrums facing south as spiders occupied east-west webs. Having the reflective dorsum facing the sun was interpreted as a means of lowering body temperature, while having the dark ventrum facing the sun was thought to be a means of increasing body temperature (Tolbert 1979). Coventry (1967) (as cited by Tolbert 1979) reported similar findings for a population of *A. trifasciata* in Wisconsin.

In contrast, magnetic headings of *A. trifasciata* at our coastal study site were never random and web placement was such that web uppersides and bodily venters generally faced the sun. The fact that spiders in our study never displayed the significant web underside/dorsum-facing-the-sun pattern described by Tolbert (1979) during hot periods, even on dates following Fridays with high ambient temperatures, suggests that dealing with a high heat load was not a significant problem. Rather, the consistent, ventrum-facing-the-sun directionality exhibited by spiders at our study site suggests that staying warm is the greater challenge. In this regard, it should be noted that this solar directionality was usually achieved by facing the plane of the web toward the sun at its noontime and sunset positions (due south; southwest), rather than toward the direction of its rising (southeast), the preferred heading in studies of two other araneids [*N. clavipes* (Carrel 1978); *Mangora gibberosa* (Hentz, 1847) (Caine & Hiebert 1987)]. This may be an adaptation to the generally overcast conditions which prevail at the Ballona study site during the morning hours (see below), which may significantly obscure the sun till it has progressed far beyond its sunrise azimuth.

We hypothesize that coastal *A. trifasciata* may seek to maximize bodily exposure to the sun in response to the cooling effects of cloud

cover and fog which typify the coastal zone (Maritime Fringe) in southern California from late afternoon until potentially noon the following morning (Bailey 1966; Schoenherr 1992). These cloud/fog layers reduce daytime solar radiation by reflecting or absorbing much of the incoming light energy and collectively truncate the number of daytime hours with unobstructed sunlight (Holland & Keil 1995). Even during the heat of the day after clouds and fog "burn off", the actual body temperatures of diurnal orb weavers at our study site may be lowered by convective heat exchange resulting from the fairly constant onshore flow of marine air which characterizes coastal Los Angeles (Bailey 1966; Schoenherr 1992).

Of course, it is also possible that magnetic heading at our study site had less to do with thermal considerations and more to do with factors such as habitat characteristics, exposure to potential predators, and prey sources, which have all been shown to influence web siting and form (Janetos 1986; Riechert & Gillespie 1986; Wise 1993). For example, large *Metepeira datona* Chamberlin & Ivie 1942 on a small Bahamian island oriented the plane of their orbs parallel to the prevailing wind, presumably to minimize wind damage (Schoener & Toft 1983). This may also be the case with *A. trifasciata* webs at Ballona, as their generally east-west planar orientation would indeed be mostly parallel to the western breezes accompanying the onshore flow. Moreover, as the radial threads in an orb web can be plasticized by contact with water (Vollrath & Edmonds 1989), potentially diminishing their ability to support both prey and the resident spider, such a facing-the-sun orientation may also facilitate the evaporation of web-borne dew/rain drops and the drying out of radial threads. Clearly, a comprehensive study involving longer-term monitoring of magnetic heading and other biotic/abiotic variables in both coastal and inland populations of *A. trifasciata* in southern California will be needed to fully assess the generality and significance of the presumed "insolation seeking" heading displayed by our Ballona population.

Inclination.—The webs of most araneids make at least a small angle with the vertical (Eberhard 1972), such that the spider's own weight pulls it away from the web's underside, which likely facilitates moving about the web

while avoiding sticky spirals (Peters 1932). What other purposes may be served by *A. trifasciata* having an inclined web is unclear in light of the present results, as well as prior studies.

Krakauer (1972) suggested inclination may have a thermoregulatory role, noting that the slight angle of *N. clavipes* webs in Florida decreases the angle through which the tip of the abdomen has to swing in order to be pointing directly toward the sun on warm days, thereby minimizing the body surface exposed to insolation. This would imply that webs which are less vertical (more inclined) may be associated with the greater insolation of summer and webs which are more vertical (less inclined) with the lower insolation of fall/winter, as a response to decreased solar heating accompanying this seasonal transition. However, Moore's (1977) May–November field study of *N. clavipes* in Texas found exactly the opposite trend, an increase in inclination over time. With *A. trifasciata* at Ballona, inclination did not exhibit either a decreasing or increasing trend and showed no relationship to the decrease in the sun's maximum altitude during the study period, suggesting no interaction between thermal factors and inclination. However, as we did not quantify posturing behavior, we can not conclusively rule out a thermoregulatory role for inclination at this time.

Eberhard (1971) proposed that the degree of inclination may be a response to wind speed, having found that orb webs of *Uloborus diversus* Marx 1898 in Arizona exposed to prevailing winds were more horizontal than webs in protected sites, presumably to minimize damage from horizontal winds. While this finding would suggest that the degree of inclination might be related to wind direction for spiders in an open setting like Ballona, the inclination of *A. trifasciata* webs was unrelated to their magnetic heading. Bishop & Connolly (1992) also found no relationship between inclination and magnetic heading for the tropical orb weaver *Leucage regnyi* (Simon 1877) in Puerto Rico. Obviously, further study of inclination and other biotic/abiotic variables in both coastal and inland populations will be needed to elucidate the factors influencing web slant in *A. trifasciata*.

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LITERATURE CITED

- Bailey, H.P. 1966. Weather of Southern California. University of California Press, Berkeley.
- Biere, J.M. & G.W. Uetz. 1981. Web orientation in the spider *Micrathena gracilis* (Araneae: Araneidae). *Ecology* 62:336–344.
- Bishop, L. & S. R. Connolly. 1992. Web orientation, thermoregulation, and prey capture efficiency in a tropical forest spider. *Journal of Arachnology* 20:173–178.
- Brussard, P.F. 1971. Field techniques for investigations of population structure in a "ubiquitous" butterfly. *Journal of the Lepidopterists' Society* 25:22–29.
- Caine, L.A. & C.S. Hieber. 1987. Web orientation in the spider *Mangora gibberosa* (Hentz) (Araneae, Araneidae). *Journal of Arachnology* 15: 263–265.
- Carico, J.E. 1986. Web removal patterns in orb-weaving spiders. Pp. 306–318. *In* Spiders: Webs, Behavior and Evolution. (W. A. Shear, ed.). Stanford University Press, Stanford.
- Carrel, J.E. 1978. Behavioral thermoregulation during winter in an orb-weaving spider. *Symposia of the Zoological Society of London* 42:41–50.
- Coventry, S.J. 1967. Web orientation in the banded garden spider, *Argiope trifasciata*. Unpublished Masters thesis, University of Wisconsin, Madison.
- Eberhard, W.G. 1971. The ecology of the web of *Uloborus diversus*. *Oecologia* 8:328–342.
- Eberhard, W.G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). *Journal of Zoology* 166:417–465.
- Felton, E.L. 1965. California's Many Climates. Pacific Books, Publishers, Palo Alto, California.
- Gould, J.L. & G.F. Gould. 2002. BioStats Basics: A Student Handbook. W.H. Freeman and Company, New York.

- Higgins, L. & K. McGuinness. 1991. Web orientation by *Nephila clavipes* in southeastern Texas. *American Midland Naturalist* 125:286–293.
- Higgins, L. E. & E. Ezcurra. 1996. A mathematical simulation of thermoregulatory behaviour in an orb-weaving spider. *Functional Ecology* 10:322–327.
- Holland, V.L. & D.J. Keil. 1995. *California Vegetation*. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Janetos, A. C. 1986. Web-site selection: Are we asking the right questions? Pp. 9–22. *In* *Spiders: Webs, Behavior and Evolution*. (W. A. Shear, ed.). Stanford University Press, Stanford.
- Krakauer, T. 1972. Thermal responses of the orb-weaving spider, *Nephila clavipes* (Araneae: Argiopidae). *American Midland Naturalist* 88:245–250.
- McNett, B.J. & A.L. Rypstra. 1997. Effects of prey supplementation on survival and web site tenacity of *Argiope trifasciata* (Araneae, Araneidae): A field experiment. *Journal of Arachnology* 25:352–360.
- McReynolds, C.N. & G.A. Polis. 1987. Ecomorphological factors influencing prey use by two sympatric species of orb-web spiders, *Argiope aurantia* and *Argiope trifasciata* (Araneidae). *Journal of Arachnology* 15:371–383.
- Moore, C.W. 1977. The life cycle, habitat and variation in selected web parameters in the spider, *Nephila clavipes* Koch (Araneidae). *American Midland Naturalist* 98:95–108.
- Peters, H. 1932. Kleine Beitrage zur Biologie der Kreuzspinne *Epeira diademata* Cl. *Zeitschrift fuer Morphologie und Oekologie der Tiere* 26:447–468.
- Pointing, P. J. 1965. Some factors influencing the orientation of the spider, *Frontinella communis* (Hentz.), in its web (Araneae: Linyphiidae). *Canadian Entomologist* 97:69–78.
- Ramirez, M.G. & K.E. Haakonsen. 1999. Gene flow among habitat patches on a fragmented landscape in the spider *Argiope trifasciata* (Araneae: Araneidae). *Heredity* 83:580–585.
- Rao, J.S. & A. Sengupta. 2001. *Topics in Circular Statistics*. World Scientific Publishers, River Edge, New Jersey.
- Riechert, S.E. & R.G. Gillespie. 1986. Habitat choice and utilization in web-building spiders. Pp. 23–48. *In* *Spiders: Webs, Behavior and Evolution*. (W. A. Shear, ed.). Stanford University Press, Stanford.
- Riechert, S.E. & C.R. Tracy. 1975. Thermal balance and prey availability: Bases for a model relating web-site characteristics to spider reproductive success. *Ecology* 56:265–284.
- Robinson, M.H. & B. Robinson. 1973. The ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology* 149:1–75.
- Robinson, M.H. & B. Robinson. 1974. Adaptive complexity: The thermoregulatory postures of the golden-web spider, *Nephila clavipes*, at low latitudes. *American Midland Naturalist* 92:386–396.
- Robinson, M.H. & B. Robinson. 1978. Thermoregulation in orb-web spiders: New descriptions of thermoregulatory postures and experiments on the effects of posture and coloration. *Zoological Journal of the Linnean Society* 64:87–102.
- Schmidt-Koenig, K. 1975. *Migration and Homing in Animals*. Springer-Verlag, New York.
- Schoener, T.W. & C.A. Toft. 1983. Dispersion of a small-island population of the spider *Metepeira datona* (Araneae: Araneidae) in relation to web-site availability. *Behavioral Ecology and Sociobiology* 12:121–128.
- Schoenherr, A.A. 1992. *A Natural History of California*. University of California Press, Berkeley.
- Schreiber, R.W. (ed.). 1981. *The Biota of the Ballona Region, Los Angeles County*. Los Angeles County Natural History Museum Foundation, Los Angeles.
- Suter, R.B. 1981. Behavioral thermoregulation: Solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. *Behavioral Ecology and Sociobiology* 8:77–81.
- Tolbert, W.W. 1975. Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *Psyche* 82:29–52.
- Tolbert, W.W. 1979. Thermal stress of the orb-weaving spider *Argiope trifasciata* (Araneae). *Oikos* 32:386–392.
- Tso, I.M. 1999. Behavioral response of *Argiope trifasciata* to recent foraging gain: A manipulative study. *American Midland Naturalist* 141:238–246.
- Vollrath, F. & D.T. Edmonds. 1989. Modulation of the mechanical properties of spider silk by coating with water. *Nature* 340:305–307.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, New York.
- Zar, J.H. 1999. *Biostatistical Analysis*. 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

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